XXXVIII. ONYCHOPHORA.

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(Plates xxxiv-xxxvii.)

Contents.

Introduction.

The discovery of a species of Peripatus on the north-east frontier of India at the foot of the Eastern Himalayas, must be reckoned as one of the most interesting zoological results of the Abor expedition. The Abor country lies far to the north of the nearest point at which specimens have previously been obtained, and no member of the group was hitherto known to occur within the limits of the Indian Empire. The single species found is, moreover, highly peculiar in many respects and, though showing traces of alliance with *Eoperipatus*, which occurs in Sumatra and the Malay Peninsula, differs sufficiently in regard to the characters employed by Bouvier, Evans and other authors to entitle it to separate generic rank; in the absence of any external trace of eyes it appears to be unique.

In describing this form it is not my intention to deal at length with the status of the different genera of Onychophora which have been proposed, or to support either of the systems of nomenclature upheld respectively by M. E. L. Bouvier and the late Dr.

Sedgwick. The species, as both authors have clearly shown, fall into groups comparatively well-defined both structurally and geographically and it seems convenient to recognize such groups by either generic or subgeneric titles. But the arrangement of these groups in separate families, as suggested by Bouvier and other authors, implies adherence to a particular view of the line which evolution has taken, and any such view, though it may ultimately prove correct, seems at present to be based on insufficient evidence.

I am therefore inclined to regard the existing species of Peripatus as constituting a single family, the Peripatidae, leaving the difficult problem of the descent of the various subgenera and genera until further information is available.

For the Abor species the name *Typhloperipatus williamsoni* is suggested. The specific name is given in honour of the late Mr. Noel Williamson, one time Assistant Political Officer at Sadiya, who was treacherously murdered by Minyong Abors on March 30th, 1911, at Komsing, a village not many miles distant from the spot where the specimens were obtained. It was owing, chiefly, to the murder of Mr. Williamson and of his companion, Dr. Gregorson, that the expedition of 1911–12 was undertaken.

Typhloperipatus williamsoni, Kemp.

1913. *Typhloperipatus williamsoni*, Kemp, Rec. Ind. Mus. IX, p. 241.

The camp at Rotung, where the majority of the specimens were found was situated at an elevation of 1320 ft. on a small plateau about 600 ft. above the Dihang River, one of the few approximately level pieces of ground seen in the Abor country. The site was at one time occupied by a village of Minyong Abors; but this was demolished in the latter half of 1911 and the villagers put up temporary dwellings half a mile further to the north at a considerably greater elevation.

The country in the vicinity of the camp was overgrown with dense scrub-jungle interspersed with stones and large trees, mostly jack-fruit. Here, as in so many parts, the ground had at one time been cleared for cultivation and the scrub, which as a rule was not more than ten feet high, probably represented some eight or ten years' growth.

It was on the eastern side of the camp on dry, gently sloping ground immediately above the edge of the great gorge of the Dihang River that Peripatus was found. In this particular spot the scrub is lower than elsewhere, exceptionally dense and interspersed with large stones and boulders. On December 29th, 1911, the first specimens, three in number, were found by my assistant, Mr. R. Hodgart, and a considerable number was subsequently obtained in the same locality.

Early in January 1912, only a few days after the capture of the first examples, it was decided to cut and burn the scrub in the vicinity of the stockade and the services of Nagas belonging

to one of the carrier corps were utilized for the purpose. Capt. T. Timbrel, who was in command of the carrier corps concerned, kindly allowed the coolies to assist in the collection of specimens, and it is entirely owing to the interest which they evinced that so large a number was obtained.

The specimens were all found under stones and this is a point of some interest seeing that all the Malayan species were found in dead wood. There was an abundance of rotten wood in the vicinity of Rotung and from it large collections of insects were made, but no Peripatus were ever discovered in such a situation. The majority of the specimens were found in chinks and crannies under comparatively large stones among the roots of jungle plants: we found it useless to search under small stones or those that were very large and deeply rooted. It needed considerable effort to obtain any number of examples, though several were often found under a single stone. Solitary individuals were occasionally met with, but more usually two to four adults accompanied by a number of young (sometimes as many as six) were collected together.

The Abor country has a very high rainfall and the expedition was undertaken during the driest months of the year. Many animals appeared to be seeking wet places in order to tide over this period of comparative drought, and the closed chambers behind the leaf-stems of plantains, where the air must always have been saturated with water-vapour, were inhabited by a large community of beetles, earwigs, slugs, snails, planarians, earth-worms and frogs; Peripatus, however, was never found in this situation.

The area in which the great majority of the specimens was obtained was very limited in extent, being about 200 yds. in length by 100 yds. in breadth. Subsequently a close search in a somewhat similar locality, situated to the N. E. near the mouth of the Sireng stream, resulted in the discovery of a few more individuals. In addition, a solitary example was found at a higher altitude by the 32nd Sikh Pioneers, while cutting a road between Upper Rotung and Renging. The distance between the two furthest points at which specimens were obtained did not exceed four and a half miles, the altitude ranging from about 1200 to 2000 ft.

Specimens were kept alive for some time in boxes; but the breeding season appeared to be over and no observations on the reproduction of the species were made. The young ones found with the adults appeared to be more or less of an age and it seems probable that reproduction takes place only during the wet season.

When touched, the specimens, as is usual in the Onychophora, ejected a semitransparent viscous fluid from the oral papillae. The discharge was directed with considerable accuracy towards the objects by which it was irritated, and was at first abundant in quantity: on succeeding occasions it was much less copious and, after a day or so of captivity, it was only by violent

stimulation that the specimens could be induced to perform the action at all. The viscous fluid rapidly solidified and formed long strings of a rubber-like consistency which adhered to everything with which they came in contact. That they never stuck to the animal itself was doubtless due to the special skin processes which, in life, give it such a deep velvety appearance.

We were never able to observe Peripatus feeding; but insects placed in the same box with it were afterwards found dead, in nearly all cases overwhelmed by the viscous secretion and firmly adherent to the earth with which the bottom of the box was covered.

When walking the antennae diverged and were held in the same horizontal plane as the body with the tips flexed a little outwards. Moving leisurely, the limbs of a single pair act in unison, having an opposite motion to those of the pairs immediately in front and behind: the claws of one pair almost touch those of the adjacent pair at each step. When moving more hurriedly the limbs of four or five adjacent pairs act together, waves of contraction and expansion pass from behind forwards, and a whole series of limbs is simultaneously lifted clear of the ground, so that the body of the animal has an undulating appearance and is only in contact with the ground in two or three places. The species walks backwards with great facility, employing the more rapid type of movement in so doing.

The limbs of the first four or five pairs are rather irregular in their motions. Those of the first pair are frequently held clear of the ground and this is generally the case with those of the last two pairs. At every step the claws are rapidly raised upwards, so that their dorsal surface touches the side of the limb. It seems that the pads are the most important organs in ordinary locomotion, the claws being of little apparent use in progression on a level surface.

External Features.

Colour.

Living specimens of adults were dorsally of a deep and rich raw umber brown colour, with the apices of the antennae for a distance of about 1 mm. of a very pale brown tint. When fully extended a small pale brown lenticular area situated dorso-laterally at the base of each antenna is exposed and on close examination the tips of all the larger dorsal skin-papillae are seen to be pale. The ventral surface, both of the body and its appendages was wholly pale brown.

In a few adults in which the dorsal colouration was somewhat lighter than that most usually met with, a very narrow black mid-dorsal stripe was perceptible and in preserved specimens, in which most of the original colour has disappeared [1], this is often a conspicuous feature. Microscopic examination shows

[1] The specimens have become quite pale after two years in alcohol.

that there is, in the middle of this stripe, an exceedingly fine pale line.

The young specimens obtained with the adults differed from them noticeably in colour. They were invariably of a pale, warm, buff tint, with the apices of the antennae pure white.

Skin.

The skin is thrown into the customary transverse folds bearing papillae. In dorsal view from 12 to 14 such folds may be counted between each pair of limbs. Towards the posterior end of the animal the interspaces between the appendages are reduced in size; the skin-folds are, however, as numerous here as elsewhere, being crowded together. The folds do not anastomoze with one another and appear at first sight to be continuous across the mid-dorsal region; they are, in reality, cut by the fine unpigmented longitudinal line referred to above. Laterally 7 or 8 skin-folds pass between each pair of limbs.

In the anterior part of the animal the skin-folds are separated by wide interspaces, which, in well-extended specimens are as broad as the ridges themselves: in this part of the body the primary papillae are small, the largest occurring laterally and on the appendages. Posteriorly the skin-folds are closely adjacent to one another, leaving practically no interspaces and in this region the papillae are considerably more numerous and frequently much larger than those on the anterior part of the animal.

The primary skin-papillae bear a close resemblance to those of *Eoperipatus*; but the round apical portion is, as a rule, less clearly separated from the basal portion than is shown in Evans' figures. In dorsal view the primary papillae have a rounded basal outline; they are confined to the skin-folds, but secondary papillae are not infrequent in the interspaces.

Antennal region.

The antennae (pl. xxxiv, fig. 1) are ringed in the usual manner. There are 27 or 28 large annulations and, except at the apex, intercalated between them, are secondary annulations, 18 to 20 in number and often incomplete. The antenna tapers from the base up to about the tenth primary annulation and from this onwards is parallel-sided. The apex is not swollen or club-shaped; but the five or six rings of which it is composed are closely packed together and are not separated by the interspaces which in the middle portion are conspicuous.

On the dorsal surface of the antenna the annulations bear small spine-tipped papillae of the usual form and larger papillae, similar in structure, are also to be found on the ventral surface in its distal half. On the proximal part of the ventral surface, however, a well-defined area, lanceolate in shape and extending from the base to about the middle of the antenna, is closely set, on both primary and secondary annulations, with papillae of a

curiously modified type. The basal portions of these papillae are round and well elevated above the general surface and their apical spines, usually very fine and slender, take the form of large broad scales with their apices directed forwards. The tips of one row of scales overlap the bases of the row immediately in front. Each scale is flat about ·25 mm. in length, lanceolate in outline and finely pointed distally; the margin is slightly roughened at the base of the apical portion (pl. xxxiv, fig. 3). There are very frequently two secondary annulations on the ventral aspect of the antenna between those of the primary series. These additional annulae, which are apparently developed in order to increase the number of scales, are restricted to the ventral surface and do not extend round to the dorsal side (pl. xxxiv, fig. 2).

The appearance of this scale-bearing patch is shown in pl. xxxiv, fig. 1, and in more detail in fig. 2, which represents a portion of the antenna viewed laterally; it constitutes one of the more striking external features of *T. williamsoni*, for a similar structure has not, I believe, been observed previously in any species of Peripatus.

The closest examination of the area at the base of the antenna and of the row of papillae which Bouvier terms the "*arceau oculaire*" fails to reveal any trace of the eye. I have also been unable to detect the "*organe frontale.*" It seems not improbable that the patch of scales on the under surface of the antenna is tactile in function, compensating in some degree for the complete loss of sight.

Buccal region.

The mouth (pl. xxxiv, fig. 1) is surrounded by large whitish lobes or tips. The lobes of the outer ring are sixteen in number, the pairs at the anterior and posterior extremities being sometimes fused. Those of the four anterior pairs bear a single spinule, while on those situated further back there may be one, two, or more rarely three such spinules. The inner ring only exists in the anterior part of the buccal opening and consists of six lobes, three on each side; the posterior pair is usually concealed by the adjacent lobes of the outer ring. The anterior lobe is the largest and bears three spinules, while the middle lobe has two. The "tongue" is longitudinally ridged and bears a single row of spinules.

The jaws are similar to those of *Eoperipatus*. On the outer blade (pl. xxxiv, fig. 4) there are two, less commonly three, accessory teeth close to the main tooth. On the inner blade pl. xxxiv, fig. 5) there are, apparently always, three accessory teeth and a series of from eight to ten small denticles separated from the accessory teeth by a short diastema.

Oral tentacles.

The oral tentacles or papillae are short and bear skin-papillae only on the lateral portions of their distal extremities. The open-

ing is surrounded by four whitish lips similar to those round the mouth.

Legs.

Of legs there are nineteen or twenty pairs. Apparently there are usually nineteen in the male and twenty in the female. I have found one male, however, with twenty legs. In the female the legs at the posterior end of the body are, as a rule less widely separated than those at the anterior end. In the male this feature is less pronounced.

The crural grooves, or openings of the coxal organs, are usually conspicuous on all the legs except those of the first and of the last two pairs. In several specimens, of both sexes, the margins of the grooves are revolute at their distal ends, forming thick, white, ∩-shaped lips.

Owing perhaps to the somewhat contracted condition of the majority of the specimens, I have found it impossible to detect the papillae observed by Evans in connection with the crural grooves. The apertures of the crural glands are visible in one individual only, a male. In this example a single, prominently exserted, white papilla, bearing the orifice of the gland at its apex, is found at the base of the two pre-genital appendages (pl. xxxiv, fig. 7).

The pads on the sole of the limb are of the usual crescentic shape and are closely covered with fine setae. On the last pair of legs there are only two pads, both small and rudimentary; on the penultimate there are three. On all the remaining legs there are four pads. On appendages in the anterior and middle portions of the body the papillae of the first transverse row below the proximal pad, though not fused together, are often transversely elongated and are beset with fine setae in all respects similar to those of the pads (pl. xxxiv, fig. 6). This row of papillae thus constitutes, in effect, a fifth pad of a rudimentary character, incomplete and much narrower than those which form the true sole of the appendage.

The renal apertures on the fourth and fifth pairs of legs are found in the third pad counting from the base of the claw. On these limbs the pad in question is completely divided into two portions, and near this division at the end of the longer and anterior of the two portions of the pad the renal orifice is situated (pl. xxxiv, fig. 6).

The foot (pl. xxxv, figs. 3, 4) is similar to that of *Eoperipatus*. On either side of the curved claws is situated a single primary papilla: one papilla being, therefore, anterior and one posterior. The papillae are conspicuous in dorsal view by reason of their large size and each is furnished with a slender apical spine. Behind the papillae the lower surface of the foot exhibits four extremely slight elevations, two, on each side, each bearing a few longish setae (pl. xxxv, fig. 4); a lateral view of the foot consequently

differs noticeably from that of *Eoperipatus*[1] in which two secondary papillae are found on each side behind the primary papilla. The elevations mentioned above do not seem to represent vestigial secondary papillae.

Ventral organs.

In the young specimens the ventral organs are distinctly seen in external examination, occurring as small whitish areas, in some of which a minute aperture is visible, in the mid-ventral line between the leg-bases. In the adults I have been unable to discover any trace of them, either on external examination or in sections.

Genital apertures.

The genital aperture in both sexes is found between the limbs of the penultimate pair. The orifice is frequently cruciform in shape and is surrounded by the customary tumid, papillose lips. The accessory glands of the male open separately, in this respect differing from those of *Eoperipatus*. The two orifices are very inconspicuous ; they are provided with small whitish lips and are placed side of side behind the base of the last pair of limbs (pl. xxxiv, fig. 7).

Internal Anatomy.

The internal anatomy of Peripatus has been so minutely investigated that it is only necessary to discuss a few points in any detail.

Nervous system.

Although no trace of the eye is visible externally the optic ganglion is well-developed and has the form of a spherical mass situated laterally at the base of the antennary nerve (pl. xxxv, figs. 1, 2, *o.g.*). The skin overlying the ganglion is wholly undifferentiated and bears papillae precisely comparable to those of the surface in the near vicinity. The epidermis is not specialized to form a cornea, the lens is entirely absent and there is no black retinal pigment.

The optic ganglion comprises a large number of ganglionic cells, but does not form a solid mass. Sections passing through it show that in the centre there is a cavity which ramifies irregularly throughout the ganglion and is lined by a loosely compacted noncellular structure. On comparison with the fully developed eye in *Peripatoides novae zealandiae* (Hutton), it is evident that the structure which lines the cavity represents the remains of retinal rods, and it appears that the ganglionic cells which originally formed a cup-shaped mass round the base of the retina have grown round the base of the rods and have completely enveloped them. The optic nerve is well-developed and is broadly expanded within the

[1] See Evans' fig. of *E. horsti*, Quart. Journ. Microsc. Sci., XLIV, pl. xxxiv, fig. 17, 1901.

ganglion. It extends backwards through the ganglionic substance of the brain, but decreases rapidly in diameter; at its actual point of attachment with the white matter it is exceedingly slender (pl. xxxv, fig. 2).

The antennary nerve appears to be considerably stouter than usual. Possibly, as some compensation for its blindness, the antennae are more sensitive in *Typhloperipatus* than in other forms. The curious scale-bearing patch on the lower surface may well be tactile in function.

The brain differs rather noticeably in shape from those of the species figured by Balfour and Bouvier. Fig. 1, plate xxxv represents a dorsal view of the entire brain in its grosser detail, reconstructed from serial sections, the white matter being indicated as a solid mass lying within the ganglionic substance, which is shown in partial transparency.

Salivary glands.

These glands are well-developed in *Typhloperipatus*, but vary considerably in length in the specimens in which I have examined them. They may extend only to the twelfth pair of legs or may reach to a point between the fifteenth and sixteenth pairs. In sections they are sometimes, but by no means always, found lying in a cavity which may have considerable dimensions. In one instance a cavity is found surrounding the posterior end of the gland; but, as far as I am able to detect, there is no communication between it and the gland: there is no such cavity on the other side of the body.

Evans writes of "coelomic end-sacs of enormous size" in *Eoperipatus* which form a most conspicuous feature in transverse sections. I presume that the asymmetrical cavity found in the Abor specimens must be homologous with these "coelomic end-sacs", but it is evident that the resemblance between the two genera is by no means close in this respect, unless the spaces should prove in both cases to be artificial. Bouvier does not seem to regard the presence of these sacs in *Eoperipatus* as a feature of any importance, since he has omitted all reference to them in his memoir.

Renal glands.

A typical renal gland from the ninth leg-bearing segment is shown in pl. xxxv, figs. 5 and 6. It consists of the customary five parts, namely the ectodermal duct, the bladder, the coiled tube, the funnel and the coelomic end-sac. There is, of course, no renal gland at the base of the legs opposite the genital opening and that of the last leg-bearing segment is but little developed in the female and, apparently, wholly absent in the male. In the male, too, the renal glands of the two pregenital segments are poorly developed, the bladder being much reduced in size and the coiled tube practically non-existent (pl. xxxv, figs. 7–10). The gland of the third pregenital segment is, however, well formed.

Crural glands.

A single crural gland is found in the male at the base of each of the two pregenital pairs of appendages. Each gland is tubular in form, often much convoluted, and placed in close juxtaposition with the renal organs of the same segment. The glands at the base of the seventeenth legs are much longer than those of the preceding segment; as will be seen from pl. xxxv, figs. 8–10, they may show considerable differences in length. Their external openings are situated a little behind those of the renal organs.

Male Reproductive Organs (pl. xxxvi).

The testes have the form of slender tubes which arise from the dorsal aspect of the seminal vesicles and extend forwards as far as the interspace between the ninth and tenth pairs of legs. They run together throughout the greater part of their length and, in the specimen figured (pl. xxxvi, fig. 1), the distal ends turn downwards towards the ventral surface, the actual apices being directed backwards.

The seminal vesicles are large sacs, sometimes 4 mm. in length; they are placed one behind the other, overlapping slightly at their point of contact, and occupy almost the whole of the body cavity between the tenth and thirteenth pairs of legs.

The vasa deferentia arise from the inferior surface of each seminal vesicle and extend backwards as a closely convoluted mass of tubes as far as the seventeenth pair of legs. At this point, in the specimen figured, the left vas deferens, that supplied by the anterior vesicle, passes beneath both nerve-cords before running forwards to join its fellow; in a second specimen one vas deferens passes under the right nerve-cord only. The two vasa deferentia, running forwards, lie close together and become enveloped in a common sheath[1], their lumina not joining until they reach the level of the eighth or ninth legs.

The common duct is of very great length, as long as the entire animal; it passes forwards from the junction of the two vasa deferentia and in one specimen reaches the fifth, in another the interspace between the seventh and eighth legs before turning backwards. The common duct has a single loop in its downward course and runs throughout the posterior part of its length on the left side of the animal. At its termination, however, between the eighteenth or penultimate pair of legs, it passes, in both specimens examined, to the right of the two nerve-cords

The testes are in an active state of spermatogenesis. The lumen, which is not sharply defined, contains quantities of sperm-mother-cells, mostly in the spireme phase. Only quite close to the seminal vesicle is any trace of the subsequent development found, the formation of the spermatozoa taking place for the most part within the vesicle. I have been unable to detect a muscular layer in the wall of the testis near its junction with the seminal

[1] They are separated in the figure.

vesicle. The vesicles themselves are full of spermatozoa in various stages of development and among them considerable numbers of sperm-mother-cells are to be found.

The structure of the vas deferens is, in one respect, peculiar. At the point where it leaves the seminal vesicle it has thick walls, the small and sharply-defined lumen being surrounded by long columnar cells with nuclei at their bases (pl. xxxvi, fig. A). It continues backwards in this character for a short distance and then rapidly changes to a thin-walled tube with a vastly larger lumen surrounded by flattened cells (pl xxxvi, fig. B). Further backwards still it returns to its original form and again becomes a thick-walled duct, while finally, before reaching the posterior limit of its length, it reverts once more to a thin-walled condition, wholly similar in structure to that found further forwards, and in this condition passes upwards and eventually joins its fellow from the other vesicle.

That two types of structure are to be found in the vas deferens is well known and sections through the thin- and thick-walled portions of the Abor species bear a close resemblance to figures given by Gaffron and Evans. But that the duct should revert to its previous condition after once having changed to the thin-walled type has not, I believe, been noticed previously in any species of Peripatus, and it is extremely difficult to suggest any reasons for such a modification.

The thick-walled portions of the duct are distinguished by oblique hatching in the central figure on plate xxxvi. In preparing this figure I was obliged to have recourse to reconstruction from serial sections, a task which, owing to the great length of the system (2500 sections were made) proved somewhat tedious: the vasa deferentia form such an intricately convoluted mass that it was found impossible to unravel them in dissection.

When the curious change in the character of the ducts was first noticed, it was natural to conclude that some error had been made in tracing their course; but a repetition of the process led to the same result and precisely similar phenomena were observed in tracing the vas deferens on the other side of the animal. It may also be pointed out that, in sections passing through the interspaces between the fifteenth and sixteenth pairs of legs, the walls of all coils of both ducts seen in cross-section are of the thin type, whereas the thick type is to be found both in front of and behind this region. This, in itself, is sufficient to prove that the thick-walled part of each duct at the posterior end of the animal must be separated by a thin-walled interval from the portion of the duct of similar structure that opens from the seminal vesicle.

The common duct, at its point of origin, is composed of an inner layer of cells of considerable depth provided with numerous nuclei and an outer muscular layer of no great thickness (pl. xxxvi, fig. C). The inner layer, which is doubtless glandular in function and is concerned with the formation of the spermatophore, increases gradually in thickness until the anterior limit of the loop of

the common duct is reached at the level of the fifth pair of legs and is at this point very densely nucleated (fig. D). On the downward course of the duct the inner layer gradually becomes thinner, the muscular coat at the same time thickening, and after looping across from the right to the left-hand side of the animal between the tenth and eleventh pair of legs the muscular envelope is very greatly developed, and from this point onwards the duct is doubtless used for expelling the spermatophores. The lumen of this ductus ejaculatorius has at first the form of a four-rayed star (fig. E), further down it changes and becomes slit-shaped, while for some distance in front of the genital aperture its outline is conspicuously lobose (fig. F).

In the material which I have examined I have not been able to find any spermatophores completely developed, but their formation in the spermatic duct is sufficiently far advanced to enable the more characteristic features to be recognized.

In every male I have examined the mass found in the lumen of the common duct is continuous, i.e. is not divided into separate spermatophores. In the case of the male figured on plate xxxvi the coating of the mass is very distinctly thickened at four points and it is clear that three separate spermatophores are in process of development. The appearance of the contents of the duct is diagrammatically indicated in fig. 2 in optical section. The mass is at several points attached to the wall of the duct by mucus.

The spermatophore would appear to be about 2 mm. in length when fully formed. Posteriorly is a large thin-walled sac in which the bulk of the sperm products are situated. The contents consist of spermatozoa, apparently embedded in a structureless matrix together with a few large pale yellowish granules. In transverse sections such granules may often be observed, along with the cut heads and tails of spermatozoa arranged in a haphazard fashion and not radiating from a central core as in *Eoperipatus* (pl. xxxvi, fig D).

In the younger spermatophores the wall of the main sac is at several points longitudinally pleated in a somewhat irregular manner[1] and this is also the case with the most fully developed spermatophore, which, however, possesses in addition a thin and smooth horny coat (fig. H).

At the distal end of the main sac the diameter of the spermatophore is slightly lessened and the wall thickened, the lumen being in consequence considerably reduced; further forward a small expansion with a thinner wall is to be found. Beyond this again the wall is very thickly chitinized and the lumen gradually disappears, giving place to a long conical cap formed entirely of chitin (fig. J). At the anterior end of the spermatophore at least four coats are to be found.

[1] This appearance is not, I believe, due to shrinkage in preservation.

Transverse sections through the anterior ends of the two less fully developed spermatophores at the point where the walls are thickening preparatory to the formation of the cap present the very characteristic appearance shown in fig. G In the case of the most fully developed spermatophore only the faintest indications of this structure can be made out, the star-shaped central portion having been obliterated in the further thickening which has taken place.

It seems that the spermatophore of *Typhloperipatus* differs from that of *Eoperipatus* in possessing a chitinous coating throughout its length and in the fact that the spermatozoa are not arranged radially round a central core. The coat is evidently a great deal thinner than that of *Peripatus*, as typified by "*P. edwardsii*" and studied by Gaffron[1], and the three to five swellings or chambers described by that author—separate receptacles in which masses of spermatozoa are accommodated—do not appear to have their counterpart in the Abor genus. The spherical globules found by Gaffron on the surface of the spermatophore do not seem to exist in *Typhloperipatus*.

But the most noteworthy feature of the male reproductive system of *Typhloperipatus* is the extremely great length of the unpaired duct. Evans in his account of *Eoperipatus* lays stress on this character and makes use of it in maintaining the close affinity of the Malayan genus with the neotropical *Peripatus*, a conclusion also accepted by Bouvier. In *Typhloperipatus* the common duct is about as long as the entire animal, much longer than in *Eoperipatus* and, in its proportional development, at least equalling that of any neotropical species.

The male accessory glands (pl. xxxvi, fig. 1, *m.a.g.*). open by separate openings placed side by side close behind the last pair of legs. They consist of simple tubes, which, however, are much convoluted. They run directly upwards from the openings and lie for the most part near the dorsal aspect of the animal, terminating blindly when they have reached the middle of the interspace between the sixteenth and seventeenth pairs of legs. In structure the glands agree with those of previously described forms; near the aperture the lumen is lined for a short distance with a thin investment of chitin.

In the possession of separate openings to the male accessory glands *Typhloperipatus* resembles *Peripatus* (American species only), the Australasian species (*Peripatoides* and *Ooperipatus*) and the S. African *Peripatopsis cinctipes*[2] (Purcell) and differs from *Eoperipatus* and all other species.

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[1] Gaffron, Zool. Beiträge (Schneider), I, pp. 152-157, pl. xxiii, figs. 62-76 (1885). According to Bouvier, Ann. Sci. nat. Zool. (9), II, p. 292 (1905), the specimens used by Gaffron for his study of the genital organs should properly be referred to *Peripatus sedgwicki*, Bouvier.

[2] According to the views expressed by Sedgwick (Quart. Journ. Microsc. Sci., LII, p. 379, 1908) this species belongs to the group "Capo-peripatus" or to

Female reproductive organs (pl. xxxvii).

It is extremely difficult to dissect out the female reproductive organs in a satisfactory manner, for the uteri, laden with the large heavily-yolked eggs and embryos are coiled within the body-cavity in such fashion that they cannot be separated in their entirety from one another or from the intestine folds of which completely fill all space superfluous to their development. The coats of the embryos and eggs, though they rupture at the slightest touch during dissection, are very impervious and I have consequently found it impossible to obtain satisfactory serial sections of the entire animal in this part of the body.

The ovary of *Eoperipatus* is described by Evans as being attached to the floor of the pericardium "not by a single ligament, but by an extensive surface, thus differing from all the genera as yet described .... It spreads itself out over the rectum and uteri like a saddle and pushes itself into any space that may be unoccupied, both between as well as outside the uteri." The ovary in *Typhloperipatus* is similar (pl xxxvii, figs. 1, 2). It lies closely pressed against the pericardium in the latitude of the sixteenth and seventeenth pairs of legs, its shape being determined entirely by the space available between the adjacent coils of the uteri and intestine. But though lying close against the pericardial floor, it does not appear to be attached immovably to it. I have found it easy to raise it from the surface and the fact that at the posterior end a well-marked funiculus is found, fused to the pericardial floor at the level of the eighteenth legs suggests that the ovary itself is in reality unattached. Evans did not find any structure resembling a funiculus in the specimens he examined, but Bouvier's account and figure of the ovary of *E. weldoni*[1] seems to show that the method of attachment in the Malaysian genus is sometimes precisely similar to that of *Typhloperipatus*: Bouvier found that the ovary was closely pressed against the pericardial floor, but was separable from it, and that it was attached posteriorly by a large funiculus.

The ovary varies from about 1·5 to 2·5 mm. in length; on external examination the follicles in which the maturing ova lie are conspicuous Anteriorly it narrows and leads into a long oviduct which is unpaired for a distance equal to more than half the length of the ovary. It divides, in the specimen figured, before reaching the level of the fifteenth legs and one branch soon afterwards bears a small receptaculum ovorum on its inner side and a large receptaculum seminis on its outer side, the latter, though it is in reality fed by two ducts, appearing practically sessile (pl. xxxvii, figs. 1, 3, 4). Similar structures are visible in the

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the genus *Peripatopsis* of Bouvier's terminology. Bouvier himself regards it as the type of a separate genus *Opisthopatus*, in which he also includes *O. blainvillei*, a Chilian species in which the openings of the male accessory glands have not been described. Sedgwick places this form in a separate group "Chilioperipatus."

[1] Bouvier, Ann. Sci. nat. Zool. (9), II, p. 365, text-fig. 34, p. 32 (1905).

other branch, the receptacula ovorum and seminis being situated, however, (in all the specimens examined) somewhat further forwards; in the individual figured they lie between the legs of the fourteenth pair. From this point onwards the uteri may be twisted together or more or less straight and soon exhibit large swellings through the thin walls of which developing embryos are visible. In the specimen figured (fig. 1) the coils of the uteri reach to the eleventh legs before turning backwards; in other examples they extend further, as far as the ninth or tenth pairs. The uteri are in all cases almost filled with developing embryos and are so closely coiled together that I have found it impossible to dissect them out in a satisfactory manner. At the posterior end of the body the uterus of each side passes round the nerve cord[1]; the two join together in an extremely short vagina and open on the ventral surface between the penultimate legs.

Transverse sections show that the ovary bears a close resemblance to that of *Eoperipatus*. The walls are very deeply folded and bear follicles containing ova in various stages of development as in the species described by Evans. The right and left ovaries are completely fused and enclose a single large cavity.

The walls of the oviduct are, in structure, closely similar to those of the ovary; they do not seem to possess a muscular layer either in the unpaired portion or when they first separate. The walls are thickened, with a consequent reduction in the size of the lumen, shortly before the receptaculum ovorum is reached and in this region a narrow muscular layer is visible Beyond this point the ducts may more properly be termed uteri; the muscular layer becomes thicker and the cells of the inmost layer are very deep and apparently take on a glandular function.

The receptacula ovorum, except for the fact that they are situated at a considerable distance from the ovary, resemble those of *Eoperipatus*. They have the form of small pouches in the wall of the oviduct and are found a little behind the receptacula seminis. They are, indeed, so inconspicuous that I was at first inclined to regard them as accidental, due to some injury or malformation of the specimen. The fact that they occur in all the specimens examined proves, however, that this is not the case. As in *Eoperipatus* there is great doubt if they ever perform the function implied by their name; no eggs have been found in them and their development, compared with that found in the neotropical species, is insignificant.

The receptacula seminis are of normal structure and are completely filled with spermatozoa The two ducts, which each possesses, are applied to the wall of the vesicle and open close together into the oviduct.

The female reproductive organs are, on the whole, closely comparable to those of *Eoperipatus*; in the complete fusion of the

[1] In all specimens examined.

ovaries they agree with this genus and differ from all other known forms of Onychophora.

The most remarkable feature of the system is the extremely great length of the unpaired portion of the oviduct. It is clear that the fusion between the right and left portions of the system, well seen in *Eoperipatus*, is still further developed in *Typhloperipatus* and this fact points to the conclusion, also indicated by other characters, that the Abor genus has reached a higher degree of specialization than its Malaysian relative.

Development.

Uterine ova in which no traces of the blastopore have yet appeared are completely filled with yellowish yolk and are from 1·5 to 1·6 mm. in length and about 1 mm. in breadth; they are consequently larger than those found in any genus with the exception of the Australasian *Peripatoides*.

The ova and embryos in any one female show a certain range of variation in age; but it seems that the whole cycle of development is not to be found in the uteri of any one individual. In one female the uteri are filled with ova in which no trace of structure is apparent. In another similar ova are to be found along with others in which some of the primitive segments are differentiated, the blastopore being either open or completely closed[1]. In other specimens only comparatively well developed embryos, bent double with the anterior and posterior ends in contact, are to be seen and but little difference in age is to be found between the embryo nearest the receptaculum seminis and that nearest the genital opening. I imagine that the subsequent stages will only be found in material collected at a later period of the year than that in which my material was obtained; I have not found any embryos which exhibit ring-like markings, nor any in which the feet are at all well developed.

It is clear that for purposes of classification on the lines adopted by Sedgwick it may safely be asserted that the uterine embryos of *Typhloperipatus* are nearly of the same age, in contradistinction to the condition found in *Peripatus*, *Eoperipatus*, *Mesoperipatus*, *Paraperipatus* and in some species of *Peripatoides* in which almost the entire cycle of development may be found in the uterus of a single female.

The distinction is perhaps not a very important one, for it appears probable that it is, in a large measure, due to climatic conditions. It seems likely that in the Abor country, with seasons well-defined both as regards temperature and humidity, young are produced at one period of the year only, probably in the wet season. In such a country as the Malay Archipelago, on the other hand, the climate is far more equable and the conditions are con-

[1] It was an examination of these specimens that led me, in my preliminary diagnosis (Rec. Ind. Mus., IX, p. 242, 1913), to make the erroneous statement that the embryos are of all ages.

sequently favourable for the production of young throughout the year.

Evans has noted that in the case of *Eoperipatus* it is difficult to imagine how the receptacula seminis obtain fresh supplies of spermatozoa, seeing that the uteri are completely filled with developing embryos and that young are apparently produced throughout the year He concludes that in *Eoperipatus* fertilization can only take place once during life; but it is not altogether clear that such an assumption is necessary. When the stock of spermatozoa in the receptacula is either exhausted or, through age, has become powerless, the production of embryos must perforce cease, giving opportunity in due course for the admission of a fresh supply. Naturally, the same difficulty does not arise in the case of *Typhloperipatus*, in which fertilization can be effected annually at the close of each breeding season.

The development of the external form in the embryo does not, so far as I have been able to determine from an examination of a limited number of stages [1], offer any very striking peculiarities.

In the manner of formation of the primitive somites there appears to be a considerable resemblance to *Peripatoides novæzealandiae* [2]. The germ-bands develop in a curved line on either side: they are widely separated from one another and between them a ventral protrusion of the yolk-mass is visible (pl. xxxvii, figs. 5, 6). I have not found any embryo at all similar to the second stage in the development of *Eoperipatus weldoni* figured by Evans (Quart. Journ. Microsc. Sci., pl. V, fig. 2, 1902).

A number of females were found to contain embryos in a comparatively advanced stage, with annulate antennae and all, or nearly all, the limbs differentiated. Two of these are figured in pl. xxxvii, figs. 7-9, illustrating the two different ways in which the embryo may be folded.

Affinities

Following the method adopted by Sedgwick in his concise account of the distribution and classification of the Onychophora (Quart. Journ. Microsc. Sci., LII, p. 379, 1908) the principal characters of the genus *Typhloperipatus* may be thus summarized:—

1. Number of legs, nineteen or twenty, variable in the same species.
2. Inner jaw with a diastema and saw of denticles.
3. Legs with four complete spinous pads.
4. Nephridial openings of the fourth and fifth legs situated on the third pad.

[1] In my material the embryos which are well preserved (fixed in hot corrosive) represent only comparatively late stages. The early stages are not in very good condition and, being exceedingly brittle, it was extremely difficult to remove them from the uteri in an entire state. I am thus not able to figure as many stages as I wished.

[2] Sheldon Quart. Journ. Microsc. Sci., XXVIII, XXIX, 1888-9.

5. Feet with two distal papillae, one anterior, one posterior.
6. Genital opening between the legs of the penultimate pair.
7. Receptacula seminis present, with two ducts opening into the oviducts.
8. Receptacula ovorum present
9. Oviducts united for some distance in front of ovary.
9*a*. Ovaries completely fused, with a single cavity. They lie closely pressed against but not directly attached to the floor of the pericardium, to which, however, they are connected posteriorly by means of a funiculus.
10. The ovary is exogenous, i.e. it is studded with follicles in which the maturing ova lie.
11. The ova are large and heavily charged with food-yolk; they measure about 1 5 mm. in their longest diameter.
12. Embryo without a trophic vesicle.
13. Uterine embryos of about the same age.
14 Unpaired part of vas deferens of very great length.
15 Spermatophores long, with horny coat and cap.
16. Skin-pigment brown, disappearing in course of time in alcohol.
17. Legs with well-developed coxal glands.
18. A single crural gland in the male in each of the two pre-genital pairs of legs.
19. The accessory glands of the male open separately on the ventral surface between the genital opening and the anus.

To these it must be added that there is no external trace of eyes and that there is a patch of highly modified scales, probably sensory in function, on the lower surface of each antenna.

The absence of eyes and the curious modifications in the antennae are doubtless to be regarded as evidence of specialization. They are not shared by any other genus of Onychophora and have consequently been omitted in the table below [1] which is intended to give a general idea of the manner in which the various genera are related.

[1] In this table I have employed the division of species, based on geographical distribution, advocated by Sedgwick (*loc. cit.*), following Bouvier's monograph in the matter of nomenclature so far as it is consistent with Sedgwick's scheme. I follow Sedgwick in placing *Opisthopatus cinctipes*, Purcell, in the S. African group, the name *Chilioperipatus* being available for the species which Bouvier refers to as *Opisthopatus blainvillei*. Sedgwick has already pointed out that *Ooperipatus*, Dendy, here merged with *Peripatoides*, is, according to Bouvier's own showing, a polyphyletic genus. Since Sedgwick's paper appeared a species of Peripatus, *P. ceramensis*, has been recorded from Ceram (Muir and Kershaw, Quart. Journ. Microsc. Sci., LIII, p. 737, 1909). This form is unquestionably to be referred to *Paraperipatus* and two additional species, also belonging to the same genus, have been described from New Guinea (Sedgwick, Nature, LXXIII, p. 369, 1910, and Horst, Notes Leyden Mus., XXXII, p. 217, 1910).

Typhloperipatus. Foot-hills of N.-E. Himalayas.	*Eoperipatus*. Malaysia.	*Peripatus*. Tropical America.	*Mesoperipatus*. Tropical Africa.	*Peripatoides*. Australasia.	*Paraperipatus*. New Britain, New Guinea, Ceram.	*Peripatopsis*. S. Africa.	*Chilioperipatus*. Chili.
Number of legs 19 or 20 pairs	23—25	23—43	23—27	14—16	21—29	16—25	19—
Number of legs variable ...	±	+	+	—	+	±	+
Inner jaw with a diastema and saw of denticles	+	+	+	—	—	—	—
Legs with 4 complete spinous pads	4	4—6	3	3	3	3	3
Nephridial openings of 4th and 5th legs on 3rd pad ...	—	+	+	+	+	+	+
Feet with two distal papillae, one anterior, one posterior ...	+	—	—	—	—	—	—
Genital opening between penultimate legs	+	+	+	—	—	—	—
Receptacula seminis present with two ducts	+	+	+[1]	+	+	—	—
Receptacula ovorum present ..	+	+	+	—	—	—	—
Oviducts united in front of ovary	+	+	—	+	+	+	+
Ovaries completely fused with a single cavity	+	—	—	—	—	—	—
Ovary attached to pericardial floor	+	+	—	+	—	±	—
Ovary exogenous .	+	—	— ?	+	+	+	—
Ova large	+	—	—	+	—	—	—
Embryo without trophic vesicle	+	—	?	+	+	—[2]	—
Uterine embryos of nearly the same age	—	—	—	±	—	+	+
Unpaired part of vas deferens of great length... ...	+	+	+	+	—	—	—
Spermatophore large, with horny cap	+	+	?	+	—	—	—
Skin-pigment brown, evanescent in alcohol ...	+	+	+	—	—	—	—
Legs with well-developed coxal glands	+	+	+	—	—	±	—
Crural glands of male in two pre-genital pairs of legs only	+	—	+	±	—	—	?
Accessory glands of male opening ventrally between genital opening and anus ...	+	+	+	+	—	±	?
Accessory glands of male opening separately	—	+	—	+	—	±	?

It is clear that the affinities of *Typhloperipatus* are primarily with its nearest geographical neighbour, *Eoperipatus*, with which, except for the unique characters mentioned above, it agrees in all important structural details but four, viz.—(i) the position of the renal openings of the fourth and fifth legs which, as in most genera

[1] It is not known if two ducts are present.

[2] According to Bouvier a tendency towards the formation of a trophic vesicle is found in certain species.

of Onychophora, are situated on the third pad, (ii) the presence of a horny coat, as well as a cap, on the spermatophore, (iii) the separation of the openings of the male accessory glands, and (iv) the similarity in age between the embryos found in a single female. It may also be noted that in *Typhloperipatus* the oviducts are united for a long distance in front of the ovary and that in the male there is only a single crural gland in each of the two pregenital pairs of limbs in place of the two found in *Eoperipatus*. In the number and position of the leg papillae and in the complete fusion of the ovaries, the Abor genus agrees with *Eoperipatus* and differs from all other known forms. It can scarcely be doubted that *Typhloperipatus* is an offshoot from the original Malaysian stock and that it is, on the whole, much more highly specialized than its allies in the Malay Archipelago and in Sumatra.

In other respects the affinities of *Typhloperipatus* seem to lie with the neotropical forms (*Peripatus*) and with those found in Australia and New Zealand (*Peripatoides*).

Evans lays stress on the points of resemblance between the Malaysian species and *Peripatus*, separating these two genera, along with *Mesoperipatus*, in a distinct subfamily. Bouvier goes still further and places them in a separate family, while Sedgwick holds the view that it is premature and inconvenient even to establish separate genera.

In *Typhloperipatus* the affinity with the neotropical species is even more pronounced than in the case of *Eoperipatus*, for it possesses several characters in common with *Peripatus* which are not shared by the Malaysian forms. Thus, the unpaired portion of the vas deferens is of much greater length than in *Eoperipatus*, being fully as long as in any neotropical species; the spermatophore is provided with a horny coat and the male accessory glands have separate openings. It also agrees with *Eoperipatus* in all the characters which that genus shares with the neotropical forms.

It seems probable, therefore, that the structure of the Abor genus will be adduced as further evidence that the views advanced by Evans and Bouvier are correct, though it is, I think, reasonable to hold that the belief in the close genetic relationship of the four genera *Peripatus*, *Mesoperipatus*, *Eoperipatus* and *Typhloperipatus*—the only interpretation that can be placed on Bouvier's classification—is not sufficiently well substantiated by the evidence available. As Sedgwick has shown, the characters of the different geographical groups or genera intermingle in a most intricate way and, in attempting to assess the value of the various combinations which are met with, it is, in the present state of our knowledge, almost impossible to determine which indicate affinity and which are merely examples of convergence.

Though agreeing in the segregation of the four genera mentioned above Bouvier and Evans hold diametrically opposed views as to the question, which is the most primitive genus now existing. A small and yolkless egg, which Bouvier holds to be the primitive condition, Evans regards as evidence of specialization,

Peripatus, according to the former author, *Eoperipatus*, according to the latter, comprising the least modified known species In effect, Bouvier maintains that the heavily-yolked eggs found in *Eoperipatus* and in *Peripatoides* are examples of convergence and for the discrimination of the "families" relies on other characters which at first sight seem less important.

Although it appears at present that the points in which the Abor and Malaysian genera show affinity with the neotropical species outweigh the characters which might be adduced as evidence of relationship with any other genus, it is possible that future research may indicate that a preponderant value should be assigned to characters based on development and in this respect the widest differences exist between the neotropical species and those found in the Abor country and Malaysia. In this event the possibility of relationship with the Australasian forms cannot be overlooked. *Peripatoides*, in the manner of its development, shows a close resemblance to *Eoperipatus* and *Typhloperipatus* and also agrees with them in many important anatomical details.

It is interesting to note that a line of migration such as would be implied in this last view is not altogether without support when the known distribution of other groups of animals is considered. Michaelsen[1] has shown that certain genera of Megascolecid Oligochaetes are found in New Zealand and India and not, apparently, elsewhere and that abundant evidence exists in this group of a faunistic connection between Australia and New Zealand on the one hand and India and Ceylon on the other. Another instance of this connection is afforded by the small freshwater prawn, *Xiphocaridina curvirostris* (Heller), which is at present known only from N.-E. Assam and from New Zealand[2]. *Xiphocaridina* belongs to the Atyidae, and is one of the most primitive genera in a family whose ancestral characters have long been recognized.

On the other hand there is a large body of evidence in favour of a faunistic connection between India and the neotropical region, traced in most cases, so far as land and freshwater forms are concerned, by way of tropical Africa. As instances of this the Aetheriidae among freshwater Lamellibranchs[3], the Cichlidae or Chromides in freshwater fish[4] and the Caecilians[5] may be cited.

It seems then that the existence of lines of migration between India and Australasia on the one hand and between India and the neotropical region, *viâ* Africa, on the other hand is in some measure established. From a geographical point of view it would therefore be possible that *Eoperipatus* and *Typhloperipatus* might

[1] Michaelsen, Mem. Ind. Mus., I, pp. 118–129 (1909) and Abhandl. Naturwiss. Verein Hamburg, XIX, 5, pp. 21–26 (1910).

[2] Kemp, Rec. Ind. Mus., VII, p. 113 (1912).

[3] See Annandale, "The African Element in the Freshwater Fauna of British India," IX Congrès Internat. Zool., Monaco, 1913, p. 583 (1914).

[4] Gunther, "Introd. to Study of Fishes," p. 534 (1880).

[5] Alcock, "Ann. Mag. Nat. Hist. (7)," XIV, p. 267 (1904).

be genetically connected either with *Peripatoides* or with *Peripatus* with both of which it also possesses morphological affinities

As the question stands at present the evidence for a neotropical connection seems to outweigh that for a migration from the Australasian region, and if we accept the view that the former has occurred, some support is given by what is known of the structure of the tropical African *Mesoperipatus*, which both Evans and Bouvier associate with *Peripatus* and *Eoperipatus*. A further study of the tropical African species may be expected to prove of considerable interest from this point of view and if any Onychophore should be discovered in S. India or Ceylon results of great importance may be anticipated.